Post-traumatic stress disorder: evolutionary perspectives

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Fear is the key emotion of post-traumatic stress disorder (PTSD). Fear's evolved function is motivating survival via defensive behaviours. Defensive behaviours have been highly conserved throughout mammalian species; hence much may be learned from ethology. Predation pressure drove the early evolution of defences, laying foundations in the more ancient brain structures. Conspecific (same species) pressure has been a more recent evolutionary influence, but along with environmental threats it has dominated PTSD research. Anti-predator responses involve both avoiding a predator's sensory field and avoiding detection if within it, as well as escape behaviours. More effective avoidance results in less need for escape behaviours, suggesting that avoidance is biologically distinct from flight. Recognizing the predation, environmental and conspecific origins of defence may result in clearer definition of PTSD phenomena. Defence can also be viewed in the stages of no threat, potential threat, encounter and circa strike. Specific defences are used sequentially and according to contexts, loosely in the order: avoidance, attentive immobility, withdrawal, aggressive defence, appeasement and tonic immobility. The DSM-IV criteria and PTSD research show substantial congruence with the model proposed: that PTSD is a disorder of heightened defence involving six key defences used in conjunction with vigilance and risk assessment according to contexts. Human research is reviewed in this respect with reference to laboratory and wild animal observations providing new insights. Understanding individual perceptual issues (e.g. predictability and controllability) relevant to these phenomena, combined with defence strategy recalibration and neuronal plasticity research goes some way to explaining why some traumatized individuals develop PTSD when others do not.
Key words: defence, evolution, post-traumatic stress disorder.

Science is facts: just as houses are made of stones, so is science made of facts; but a pile of stones is not a house and a collection of facts is not necessarily science.

Henri Poincaré, 1842–1912.

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Survival perspectives

Disordered emotions have been a key focus of psychiatry. Evolutionary psychology views emotions as response patterns shaped by natural selection to offer selective advantages in certain situations [1]. Emotions motivate survival behaviours. Fanselow and Lester described '..the organism as confronted with a series of environmental problems that must be solved to insure future reproduction' [2].

Many features of anxiety disorder subtypes correspond to dangers encountered recurrently by our distant ancestors [1,3,4]. Anxiety is a response to potential threats, while fear relates to direct threats. Anxiety involves less organized behaviour than fear.

Phobias, despite being listed in DSM-IV as anxiety disorders, relate to direct threats [5,6]. The neural circuits of anxiety and fear are distinct. Fear involves primitive structures in the hind-brain, for example the periaqueductal grey. Anxiety, unlike fear, activates the hypothalamo-pituitary–adrenal axis [7]. Fear is the key emotion in post-traumatic stress disorder (PTSD) and its function is motivating defence. Therefore, might PTSD be a disorder of defence?

That PTSD is noxious and disabling does not automatically negate a potentially adaptive function. People born without capacity for pain die early. Diarrhoea and vomiting are unpleasant but their aversiveness drives future avoidance. The clinician's illusion is that symptoms are the problem [8]. Importantly for understanding evolution and PTSD, what is adaptive in one environment may not be so in another.

The more essential a characteristic is for survival the more it will be conserved over evolutionary time. The basic skeletal design of a vertebral column, ribs and four limbs has persisted over many millions of years in virtually all higher animals. Significant qualitative changes in design would tend to be fatal, although there has been scope for adjustments. Fundamental survival behaviours include breathing, eating and sexual reproduction, with remarkable similarities throughout the animal world. Defence is another fundamental of survival; hence it too is highly conserved [3], although the defence repertoire of higher primates is more complex [9].

This paper explores ethological research for insights into defence and PTSD. The framework of an evolutionary theory of PTSD integrating existing behavioural, information processing and neuroscientific theories is presented. Not only is evolutionary theory unfamiliar to some researchers and clinicians, but the topic of evolution and PTSD is also very recent. Marks' landmark 1987 work on evolution and anxiety disorders paid only modest attention to PTSD, which was then in its infancy [10]. Subsequent PTSD-specific work has included Silove (1998) [11], Cantor (2005) [3], Bracha *et al.* (2005) [12] and Cantor and Price (2007) [13]. The basic principles of the evolution of defences will be considered before examining their relevance to the psychopathology of PTSD and briefly presenting insights arising from a defence perspective. Potential explanations for the enduring nature of PTSD will be suggested.

Predation and the evolution of defences

All current life on earth originated from unicellular organisms that, despite the absence of nervous systems, could learn defensive strategies [10]. Adaptive decision-making has been demonstrated in both vertebrates and invertebrates [14]. Even simple prey such as insects make defensive decisions and respond accordingly. In the journey from early unicellular organisms of 3000 million years ago to modern *Homo* a few hundred thousand years ago milestones included the arrival of early reptiles and mammals 300 and 200 million years ago, respectively. Primary motivational neural circuits in the brain developed early in evolutionary history, in primitive cortical, subcortical and midbrain structures mediating largely unconditioned essential survival behaviours [5]. These primitive structures include the amygdala and its projections. For a review of the relevant neuroanatomy and neurophysiology see Davis [15].

Neurologist Paul MacLean developed the 'triune brain' concept, which suggests that both anatomically and functionally the human brain reflects three ancestral eras of development: the reptilian; palaeo-(old) mammalian; and the neo-(new) mammalian eras, with the latter emerging 65 million years ago following the mass extinction of large reptiles and dinosaurs [16]. The corresponding brain regions and functions essentially are reptilian behaviours, palaeo-mammalian emotions and neo-mammalian reasoning. The triune regions may operate in isolation or concurrently.

Defence can be viewed as having three foundations: threats posed by predators; conspecifics (same species); and the environment. Predation laid the essential foundations and has also been a major driver of general organismic complexity [17]. Predators may influence prey populations by stimulating costly defensive strategies, with intimidation affecting prey numbers at least as much as prey consumption [18]. Conspecific pressure is relevant to more recent defence evolution.

Most PTSD literature is based on conspecific research, particularly of war veterans, and the results may not be representative of other PTSD populations. Might predator-induced PTSD differ from conspecific-induced PTSD? This could be studied using large cat or shark attack file data sources. Might shark attack victims display less generalized avoidance, particularly less fear of conspecifics, but a more specific sea phobia? Although PTSD studies to date have not addressed the predator question, rates of conspecific-induced PTSD (assaults) tend to be higher than environmental PTSD [19]. Although it has been suggested that this may relate to disillusionment with humanity and loss of trust, the subcortical brain structures involved in PTSD suggest alternative explanations.

Successful predation requires five components: detection, identification, approach, subjugation, and consumption [20]. Prey anti-predator responses mirror these. Reptiles

use more diverse, less energy-demanding responses than mammals, which have greater energy capacity [21]. Mammalian defences are less diverse but are more widely distributed throughout mammalian species [22]. Nevertheless, because reptiles preceded the advent of early mammals by 100 million years the foundations of some mammalian defences have reptilian origins, with more automatic and rapid, as opposed to consciously calculated responses [16,23].

Anti-predator traits span behaviour, morphology, physiology, chemistry and life history [24]. There are two main behavioural strategies: predator avoidance and predator escape from being consumed. Avoidance involves avoiding a predator's sensory field, the latter evading detection within a predator's sensory field and escape. Avoidance and escape are separate functional entities. Avoiding a predator's sensory field involves some prey spending much of their lives in refuges and/or reduced activity, such as emerging at particular times of the day.

Avoiding detection within a predator's sensory field may entail morphological or behavioural crypsis (concealment) [24]. Prey can recognize predators and change their behaviours accordingly. Rodents may forage around shrubs when under threat from owls, but switch to the open when under threat from snakes [25]. Following predator detection more active defences such as withdrawal or aggressive defence may be used for capture deterrence. Let us now examine the key defences.

Defence hierarchy

Marks described four fundamental mammalian defences: withdrawal, immobility, aggressive defence, and appeasement [10]. He described two types of immobility – attentive and tonic – with little in common except immobility. He noted that avoidance, withdrawal, flight and other escape behaviours comprised a broader avoidance strategy. For reasons that will later become clear I shall follow Langerhans' separation of avoidance from withdrawal [24]. Hence, the traditional oversimplistic 'fight or flight' should be re-conceptualized as six key defences in a specific sequence: avoidance, attentive immobility, withdrawal, aggressive defence, appeasement, and tonic immobility [3]. All six defences are routinely complemented by vigilance and risk assessment.

Studies of US, Brazilian and Welsh students have demonstrated that people use similar defences to rats, the most convenient laboratory research animal. Defence, however, is less conditioned and more innate in less encephalized mammals [6].

The notion of six key defences is usefully complemented by the concept of a distance-dependent defence hierarchy [2,3,26,27]. Prey defensive decision-making is determined by the distance from predator, the predator's behaviour and cost–benefit calculations regarding access to food or mates [28]. The combination of physical and psychological distance variables is referred to as 'predatory imminence' [2].

Stage 1 of the distance-dependent hierarchy involves prey engaging in its preferred activity in the absence of predation (or other threat). Stage 2 is a pre-encounter scenario involving potential threat. Stage 3, after encounter, involves predator detection. Stage 4 is circa-strike defensive behaviour [2,26,29]. A fifth stage, recuperation from wounds by lying low until the period of threat has passed, has been suggested [30].

The hierarchical approach positions avoidance in the first and second stages – preferred activity and potential predation threat – whereas flight belongs in stage 3: after encounter. An important implication is that the more successfully an early strategy is used, the less the need to rely on later strategies. Nowhere is this more apparent than in the tortoise whose unusual withdrawal of body parts into its carapace has eliminated the need for energy-demanding flight or fight. Avoidance and flight have been driven by distinct selection pressures and their biology will reflect this. Understanding this is important for considering the confused DSM-IV avoidance-behaviour criteria that reflect true avoidance, withdrawal and numbing phenomena.

Marks was clear that the two immobilities – attentive and tonic – are different physiologically and functionally [10]. Brandao et al. claim to have identified the neural substrates of at least four different types of immobility, but their work is difficult to incorporate with functional research [7]. It is sufficient to recognize that attentive immobility occurs early in the defence sequence, whereas tonic immobility is the last defence prior to consumption.

The post-encounter stage of flight or fight is associated with sympathetic activation [31]. Flight or other withdrawal will generally be preferred to aggressive defence because it carries less risk of injuries that may hamper foraging or predation, decreasing survival.

Appeasement is primarily a defence for conspecific encounters with more dominant individuals. It involves pacification, conciliation and submission [3].

The final circa-strike defence is tonic immobility. It involves a sudden prolonged stillness with preservation of awareness. It is initiated by inescapable situations, often with physical contact, particularly restraint [31]. It involves zero or near zero distance and immediate predatory imminence.

While I refer to the six key defences as avoidance, attentive immobility, withdrawal, aggressive defence, appeasement, and tonic immobility, all these defences involve

the vital co-phenomena of vigilance and risk assessment. Whereas psychiatry has tended to equate hypervigilance with physiological overarousal, ethologists view hypervigilance more in terms of watchfulness. Vigilance increases as risks are assessed as greater or ambiguous [32]. In primates much vigilance may relate to defence against conspecifics as opposed to predators [33].

Post-traumatic stress disorder and DSM-IV

Let us now examine the relevance of these issues to the clinical phenomena of PTSD. The DSM-IV stressor criteria involve threat of death, physical injury or a threat to the bodily integrity of oneself or others [34]. Hence, defence is highly relevant to the stressor criteria.

All five re-experiencing criteria (intrusive recollections, nightmares, and the three criteria relating to heightened reactions to trauma memories) [34] reflect enhanced memory for threats. Re-experiencing phenomena keeps defence in the foreground of concerns. Sullivan and Gorman have suggested that PTSD is a disorder of fear memory circuitry [35]. Silove described survival benefits from a rapid and enduring fear learning system with cortical and subcortical pathways [11]. In mice memory of electric shocks in the immediate aftermath predicted re-experiencing symptoms but not avoidance or overarousal symptoms [36].

The DSM-IV avoidance C criteria [34] sound more encouraging for the theory than they actually are, but there remains considerable congruence. Criterion C1, avoiding thoughts, feelings or conversations associated with the trauma, is more consistent with psychological flight than avoidance. Criterion C2, avoiding activities, places or people arousing recollections of threats is clearly consistent with defence. Strictly interpreted it is unclear whether this criterion would include flight, but most patients fleeing from trauma reminders will also avoid them. C3, psychogenic amnesia, also represents psychological avoidance/flight.

C4, diminished interest or participation in significant activities, C5, feelings of detachment from others, and C6, restricted range of affect, are somewhat problematic. Foa *et al.* suggested that these are numbing symptoms that should be separated from avoidance behaviours [37]. Numbing involves the opioid system and relates to the stage 3 post-predator encounter [2]. Numbing of injuries inflicted by predators facilitates flight or fight, flight to a refuge and avoidance of coming out. Hence, numbing is more an adjunct to these defences than an independent entity.

C7, a sense of foreshortened future, appears depressive. A shortcoming of the current approach to PTSD is the non-specificity of the word 'trauma' that includes fear, loss and other noxious emotions. PTSD might be more useful if it was restricted to the emotion fear; loss is adequately catered for by depression.

The D overarousal symptoms [34] are sometimes referred to as hypervigilance phenomena, and criterion D4 is just that. D5 relates to startle reactions, which involve rapid automatic withdrawal and aggressive defence responses from lower brain areas. They are considered reliable indicators of fear in fear research [5]. Delays associated with emotions and reasoning may prove fatal so primitive rapid reptilian functions are highly represented in defensive behaviour.

Criterion D1, sleep disturbance, is consistent with hypervigilance but would be more useful if described specifically as a sleep disturbance associated with safety concerns, differentiating it from depressive insomnia. D3, difficulty concentrating, is similarly problematic, involving concentration on safety at the expense of other issues. This leaves D2, anger/irritability, which clearly relates to aggressive defence.

Hence, the still evolving criteria due for revision for DSM-V include the theory's memory component for a heightened state of defence; the vigilance aspect and, in a muddled way, avoidance, flight, numbing and aggressive defence phenomena. There is a remarkable degree of fit with the evolutionary theory. But what about appeasement and the immobilities? The theory is jeopardized if these are not found in PTSD. Cantor and Price have suggested that appeasement is the foundation of complex PTSD [13]. The paradoxical attachments of abused children and spouses to their abusers and those of Stockholm syndrome victims are understandable when viewed from the perspective of appeasement.

This leaves attentive and tonic immobilities. The next section briefly provides some insights from this defence perspective, prioritizing tonic immobility because it is unfamiliar to many clinicians.

Clinical insights from defences

Avoidance

Avoidance of predators, conspecific and environmental hazards involves avoidance of entering the relevant field: stage 2, a pre-encounter scenario [2]. Avoidance was the dominant defence in the energy-limited reptilian era, flight and fight being energy demanding. Hence, avoidance

should have significant neurodevelopmental representation in the human 'reptilian' brain. Sure enough, the brainstem basal ganglia and extrapyramidal motor systems control a number of automatic behaviours [38]. The reptilian quality of avoidance in PTSD may result in patients defaulting on exposure challenges for reasons lying outside of awareness (although palaeo- and neo-mammalian correlates may co-occur).

Asking potential PTSD patients how they cope with supermarkets and crowded shopping centres is useful. They frequently avoid them. What are the contextual implications of this? Environmental dangers seem irrelevant. Predation threat would be only symbolically relevant; many noisy people may alert predators. Conspecific fear of strangers appears more relevant.

Avoidance involves modification of behaviour according to the perceived likelihood of a threat encounter: a cost–benefit calculation. This has been explored experimentally using the size and frequency of rat meals. Frequent small meals are preferred because they are digested more efficiently, but carry risks associated with time away from the burrow. As the perceived risks experimentally rose, rats switched to larger, less frequent, less digestible meals with the benefit of less exposure to predators [2]. The pregnant female of some species take more risks with predators compared with the stronger male [37] because they have greater nutritional requirements, again illustrating cost–benefit calculations [14]. Well-nourished pregnant humans with PTSD are unlikely to display less avoidance in the absence of predators, but the hypothesis would be readily testable.

Attentive immobility

Attentive immobility is a transitional state of high arousal and hypervigilance that follows detection of a possible immediate threat [38], that is, stage 3 – after encounter – and is a prelude to definitive defence decision-making [14]. Attentive immobility keeps the head still for careful assessment of threat, provides crypsis and primes the individual for flight or aggressive defence [21]. Attentive immobility involves focused attention, cardiac deceleration, analgesia and potentiated startle [32]. Bradycardia is sufficiently reliable that along with measurements of body sway (an index of immobility) it has been used in human investigations of attentive immobility [39].

Attentive immobility is particularly pronounced in rats, making them useful research subjects, but it is a familiar human experience, unlike the unfamiliar tonic immobility. Defensive aggressive behaviours, including startle, in wild rats were found to rise abruptly as predator–prey

distance decreased, suggesting an increase in muscle tension with attentive immobility [22,40]. Attentive immobility is mediated by the lateral projections of the central grey that also mediates stress-induced analgesia [41].

Withdrawal

Reptiles have limited energy reserves for energy-demanding defences such as flight and aggressive defence. When reptiles do use flight it requires augmentation by withdrawal to refuges such as cracks in rocks inaccessible to predators [21]. Aquatic insects, gastropods, crustaceans, fish, reptiles and mammals have all been observed to use refuging [42]. Refuging increases with rising predation risk [14] and is likely to similarly increase with conspecific risks.

Although human refuging may have ancient reptilian origins, it could also have arisen through evolutionary convergence, which involves a shared solution to an evolutionary challenge, without shared ancestral inheritance of the strategy. The hovering long-tongued humming bird and humming bird hawk moth use the same solutions for reaching nectar in deep flowers without suitable perches. One is a bird, the other an insect. The slow flight of primates has been a recent development from our faster mammalian ancestors, suggesting possible refuging by convergence. Fast-footed mammals that can outrun predators utilize open spaces for defence. Refuging includes both flight to refuges and avoidance of emerging for extended periods, to ensure that dangers have passed.

Patients with PTSD often talk more about refuging than about flight. They gain a greater understanding of their withdrawn, often near-housebound states when they understand that this relates to not only avoidance in the DSM sense, but also in the defensive sense. Non-human primates seek refuges up trees; humans use their homes.

Refuging lends itself well to research because different PTSD sample groups may present different activity schedules. Comparing environmental- versus conspecific-induced PTSD with respect to proportion of time spent within the home would be simple, but ethological hypotheses are preferable to intuition.

Flight initiation distances from predators were found to increase with distance from burrows in woodchucks and took into account the positioning of the predator with respect to the woodchuck and the burrow [43]. This again illustrates cost–benefit calculations with respect to interrupting foraging and the use of energy-demanding defences. Risk assessment is pharmacologically distinct from flight: flight decreases selectively with anti-panic drugs while risk assessment responds to anxiolytics [6].

Aggressive defence

Aggressive defence is subdivided into aggressive signalling and the more dangerous 'fight'. Anger is an emotion with exceptionally effective signalling functions [44]. Only if signalling fails is the more energy-demanding and hazardous fight response likely to be initiated [3,10]. Prey may alert predators that they have been detected by attempts to frighten, confuse or intimidate them [24]. Prey may use aggressive signalling as part of an escape response, combining fight with flight. Aggressors signal aggression with conspecific encounters but not when attacking prey as they strive to remain undetected.

Appeasement

Cantor and Price recently published in this Journal a detailed review of appeasement reactions, providing animal and human observations suggesting that appeasement is the foundation of complex PTSD [13], and so I only make brief mention of it here. Appeasement's association with conspecifics suggests a more recent triune brain heritage than defences evolving from predation.

De-escalation is one of appeasement's core functions [45]. Defeated primates have been observed to retreat, only to return to the dominant conspecific and protest until signals of acceptance are elicited, a phenomenon known as 'reverted escape' [46]. It involves flight to the source of the threat. The dominant may engage in further coercion, with the subordinate responding with more appeasement, reinforcing their social bond with due recognition of status. This is commonly observed with abused spouses and children [13]. From an evolutionary perspective subordinates often have to maintain group membership for survival, and dominants need to maintain group cohesion.

A specific traumatic context, traumatic defeat plus an inescapable relationship with a dominant oppressor, resulting in specific PTSD symptoms, suggests that PTSD research may benefit from greater consideration of contexts: predator, conspecific and environmental, combined with other contextual characteristics. This might lead to greater understandability and predictability of treatment responses. It contrasts with a general malfunctioning disease-based approach. 'PTSD' may be better viewed as the 'PTSDs' (plural).

Tonic immobility

Tonic immobility is the final defence in the chain of anti-predator responses: nature has one last desperate measure [47]. It is widely represented throughout the animal world in insects, crustaceans, fish, amphibians, reptiles, mammals and birds [27,31]. It arises in situations of immediate 'predatory imminence' (and its conspecific or environmental counterparts). It is an involuntary state of profound motor inhibition despite fully preserved consciousness, activated by extreme fear, perceived inescapable circumstances, usually involving an obviously more powerful predator or conspecific [3,48]. In animals it usually involves restraint. On termination of tonic immobility sudden recovery and flight may occur but this is neither as precipitous nor as reliable as that following attentive immobility [10]. Tonic immobility may persist beyond release [27] and in chickens has been observed to last up to 5¾ h [49].

It may promote survival through inhibition of predator killing reflexes, confusion of predators, deterrence through raising the possibility of diseased dead meat and lowering of blood pressure, which reduces blood loss from injuries [3,31]. With conspecifics its submissive aspects may serve also as appeasement to deter more serious assault.

During tonic immobility animals remain largely unresponsive to external stimuli. The immobility involves either muscular hypo- or hyper-tonicity, waxy flexibility, suppression of vocal behaviour, intermittent eye closure, Parkinsonian-like tremors with changes in heart rate, decreased temperature, increased respiratory rate and electrocardiogram changes [27,49,50]. Experimental pre-induction shocks stimulating fear and/or adrenalin injections can greatly extend tonic immobility, whereas increasing familiarity with the threat decreases it.

Waxy flexibility in combat victims presenting with tonic immobility may be misdiagnosed as psychotic catatonia [51]. There are many similarities and differences between tonic immobility and catatonia [52]. Tonic immobility evolved as a fear response for present threats. With humans such responses may be activated by fear but maintained by a cognitive focus on potential (i.e. future) threats, with those threats remaining undetected, resulting in a protracted state of immobility commonly described as catatonic stupor. The linkage of catatonia with defence against ill-defined threats is further supported by catatonic excitement being associated with undirected assaultativeness.

Some conversion reactions may reflect animal defence behaviours [12,53]. Accounts of the immobility involved in World War I shell shock are often difficult to differentiate between catatonia, conversion or tonic immobility. Some support for this arises from neurophysiological findings of hyperactive monitoring during motor-initiating decisions in subjects with conversion paresis of one arm [54].

In contemporary humans tonic immobility is commonly experienced with conspecific encounters in rape-induced paralysis [27,30,55]. A total of 37% of 35 rape victims were found to have experienced tonic immobility [56]. It also has been found in victims of other sexual abuse and some non-sexual violence. Heidt *et al.* found that 52% of women with histories of childhood sexual abuse reported tonic immobility in response to the abuse [57]. Older perpetrators and greater age differentials (suggesting perceived inescapability) between the abusers and children were both associated with greater tonic immobility, which was associated with greater distress, peritraumatic dissociation, depression, anxiety and PTSD. Similarly, 41.7% of survivors of adult sexual assault reported significant immobility during their most recent assault, and 10.4% reported extreme immobility [58]. Rape victims may be insensitive to pain during tonic immobility [27].

Tonic immobility may be a key determinant of PTSD outcome following sexual assault. Tonic immobility was found to partially mediate the relationship between fear and both overall PTSD symptom severity and PTSD avoidance/numbing [49]. Further, the relationship between perceived inescapability and PTSD symptom severity and avoidance/numbing was fully mediated by tonic immobility. No relationship was found between tonic immobility and hyperarousal symptoms, suggesting that, like appeasement, tonic immobility may generate specific PTSD symptomatology and that tonic immobility-driven PTSD may be less responsive to arousal-lowering treatments.

Non-sexual conspecific assaults have also involved tonic immobility, with 43% of victims of urban violence reporting peritraumatic tonic immobility, which emerged as a marker for poorer responses to psychotropics [59]. Tonic immobility, but not dissociation or panic, predicted PTSD symptom severity after controlling for potential confounders in urban violence victims [60].

The preservation of awareness with an inability to voluntarily respond implies dissociation [3]. Depersonalization (detachment from self) but not derealization (detachment from environment) was found to be associated with tonic immobility, but the reverse occurred with fear [58]. This fits with depersonalization having an internal focus on why one is not responding, whereas in derealization the focus is more external. Dissociative identity disorder patients often become immobile, enter trance-like states and report out-of-body experiences or dissociative amnesia [30]. While tonic immobility is not associated with all types of dissociation, might there be a subtype of dissociation specific to tonic immobility?

Enduring defensive reorientation

PTSD involves an enduring heightened defensive orientation. What causes this in some trauma victims but not others?

Perception, controllability/predictability and contexts

The significance of traumatic events differs for different individuals. The traditional model of PTSD linking threat exposure to psychopathology neglects the appraisal process in humans that links an objective event to a subjective response [61]. How a traumatic event is processed [3,62,63] depends on complex interactions between an individual's psychological makeup, the traumatic event and the context in which it occurs.

Conditioning research has tended to overlook the contexts in which aversive stimuli have been applied [63]. Aversive stimulation in laboratories is associated with longer lasting changes than in the wild, possibly because wild animals have trade-offs to consider: the costs and benefits of strategies in complex and dangerous environments [64]. Bearing in mind that PTSD in war veterans often becomes more overt following repatriation, might the cost of avoidance for combat veterans be too great until they have left the war zone? In laboratory animals environmental variables predispose and increase responsivity, and lack of social interactions may increase the consequences of aversive experiences and inescapability [64]. This is akin to child abuse and neglect being risk factors for adult human PTSD.

Trauma processing will be influenced by gene-neural variance, life histories, predictability, controllability, and other individual and contextual variables [3]. There is strong evidence that controllability and predictability are crucial psychological variables [65]. Studies of laboratory animals and torture victims have shown that even an illusion of control can be protective [66]. PTSD may even occur with the deprivation of control in prisoners in the absence of actual physical torture [67].

Overlapping with controllability/predictability issues is that of mental defeat, which is the perceived loss of all autonomy, a state of giving up efforts to retain one's identity with an independent will [19]. It represents the complete breakdown of resistance to the oppressor. Torture victims may face uncontrollable external circumstances yet remain mentally undefeated: 'I'm going to die — so be it.' Mental defeat in East German political prisoners was correlated with both the development and severity of PTSD.

Unconditioned behaviours and preparedness

Newborn infants do not learn to breath, they simply do it. Breathing is an unconditioned behaviour fundamental to survival. Laboratory-bred rodents that have never met predators respond on first exposure to predator cues with risk assessment behaviours, freezing and withdrawal [64].

Other defensive behaviour may be rapidly learnt or activated by a process that Seligman called 'preparedness' [68]. Laboratory-reared monkeys were initially unafraid of snakes, but rapidly became fearful following viewing wild adult monkeys responding fearfully to snakes [69]. Their rapid fear learning was prepared by evolution.

Short aversive stimulation increases defensive behaviour in animals including risk assessment, freezing, escape, withdrawal, general activity and social behaviours. A single aversive event may result in lasting shifts in response patterns. Inescapable shocks were found to increase defensive behaviour for up to 10 weeks [65]. Exposure of rats to cats resulted in changes of up to at least 12 days in anxiety-like behaviour, potentiated startle and amygdala hyperexcitability [70]. Animals may associate both the aversive stimuli and the contextual cues with threats, resulting in generalization as seen in PTSD [63].

Agonic switching and plasticity

Defensive reorientation following threats may also occur at a social systems level. Humans usually operate under a 'hedonic' orientation. The hedonic mode involves affiliative relationships with cooperation and facilitation of exploratory behaviour [44]. The latter facilitates mate-seeking and food-gathering but is the opposite of defence. At times of heightened threat a switch to the agonic mode may be adaptive. This involves interactions based on competition with resolution based on dominant subordinate polarities. Some social animals such as wolves are more routinely orientated to the agonic mode. Populations of individuals with genetic makeups allowing for flexibility in these regards will have survival advantages. While the agonic orientation of PTSD may be mostly unhelpful in contemporary humans for whom the frequency of threats is usually low, if the environment were to become more threatening, constitutional flexibility for switching to a more defensive mode might be adaptive.

An optimal defence system will involve many false alarms [8]. The smoke detector principle notes that false alarms are inexpensive compared with dire consequences in the absence of alarms. An optimal defence system involves a lower cost of using a defence than the cost of not using it. Recalibration may occur according to the frequency and/or severity of threats, and control systems do not necessarily return to their previous levels.

Enduring agonic switching would be expected to have some physiological representation. Langerhans observed the following [24].

> *Many prey organisms have evolved adaptive predator-induced phenotypic plasticity, where particular phenotypes are only produced under the threat of predation, thus avoiding fitness costs in the absence of particular predators. Others have fixed phenotypes. Plasticity will be favoured in changeable environments, where environmental cues permit predicting cost-benefits.*

Neural plasticity in afferent projections to and efferent projections from the amygdala seem to mediate lasting consequences of aversive stimulation. Neurotransmitter gastrin-releasing peptide (GRP) increases GABAergic inhibition in lateral amygdala during extinction of conditioned fear. When GRP release is prevented, fear memory persists [64]. In the generation of psychopathology overactivation of such circuits with resulting sensitization is one possibility, memory modulation is another. PTSD might result when the extinction of an aversive event's psychobehavioural response is impaired. Memory suppressor genes and other molecular and cellular mechanisms might operate. Different experience-dependent synaptic plasticity may be associated with outcome.

Ethology

Ethological studies of wild animals are important for exploring evolution and PTSD. The absence of PTSD in animals would cast doubt on the theory proposed. Demonstrating its existence may clarify the core features of PTSD. Laboratory animal models generally involve elements of PTSD-like states without true PTSD. Ethologists have barely considered PTSD in wild animals. There has been a recent report, however, of possible PTSD in elephants [71]. It is difficult from the description of the disturbed behaviour – both fearful and aggressive – to be sure that it represents PTSD, but it seems a possibility. There also has been a convincing report of complex PTSD in chimpanzees rescued from years of traumatic entrapment in research laboratories [72]. Our relatedness to elephants is relatively distant but we are close to chimpanzees. Elephants, like humans, however, are socially

complex and caring creatures. Elephants may also display both long-term predispositions from early life trauma, much the same as seen in abused children at risk of adult PTSD. Elephants' early developmental environments are now often so profoundly disrupted by poaching and culling that matriarchs and allomothers are eliminated from herds. Female elephants now may reproduce at abnormally young ages, and do so as stressed, inexperienced, single mothers without the socioecological knowledge, leadership and support from matriarchs and allomothers [73]. PTSD has been detected in elephants in part because their size, territorial mobility and loss of habitat has brought them into conflict with humans. The refuging of PTSD in most wild species renders them relatively invisible, making field studies a challenge.

Conclusions

A defence-based model of PTSD is proposed. Fear motivates defensive behaviours, the chief of which in mammals are deployed sequentially according to distance from the source of threat and other contextual variables. Those defences are avoidance, attentive immobility, withdrawal, aggressive defence, appeasement, and tonic immobility operating in conjunction with vigilance and risk assessment. PTSD may have involved an enduring heightened defensive reorientation that has been adaptive. The evolutionary perspective brings together psychological, social systems and neuroscientific research findings.

> *False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for every one takes a salutary pleasure in proving their falseness: and when this is done, one path towards error is closed and the road to truth is often at the same time opened.*
>
>   *Charles Darwin, The Descent of Man, 1871* [74]

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